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Ammospermophilus harrisii.

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Ammospermophilus harrisii (Audubon and Bachman, 1854)

Harris' Antelope Squirrel

Spermophilus harrisii Audubon and Bachman, 1854:267. Type locality restricted by Mearns (1896:444) to "the Mexican boundary line, from the Santa Cruz Valley westward as far as the Sonoyta," Arizona.

Ammospermophilus harrisii: Mearns, 1907:303. First use of current name combination.

CONTEXT AND CONTENT. Order Rodentia, Suborder Sciuromorpha, Family Sciuridae, Tribe Marmotini, Subtribe Ammospermophilina (Hafner, 1984). The genus Ammospermophilus contains five species; A. harrisii, A. insularis, A. interpres, A. leucurus, and A. nelsoni. A key to the species is presented in Best et al. (1990). A. harrisii contains two subspecies (Hall, 1981):

- A. h. harrisii Audubon and Bachman, 1854:267, see above.
- A. h. saxicolus (Mearns, 1896:444). Type locality "Tinajas Altas, Gila Mountains, Yuma County, Arizona" (kinoensis Huey is a synonym).

DIAGNOSIS. Ammospermophilus harrisii (Fig. 1) differs from other similar-sized ground squirrels by its grayish dorsum and tail and by the presence of one white stripe along both sides of the body from shoulder to rump (Caire, 1978). It is distinguished from other members of the genus by the mixed black and white undersurface of the tail; other Ammospermophilus have a white undersurface of the tail (Hall, 1981). The percentage of light reflected from the mid-dorsal surface, for various wavelengths, is less for A. harrisii than for either A. leucurus or A. interpres (Findley et al., 1975). A. harrisii is distinguished from A. leucurus by pelage color (usually darker and grayer), and especially by the banding pattern on the undersurface of the tail (salt and pepper gray compared to white surrounded by one black band in A. l. leucurus). Cranially, the two are similar, but A. harrisii has slightly larger auditory bullae (Hafner, 1981).

GENERAL CHARACTERS. Ammospermophilus harrisii is medium in size. The tail is medium to short and the ears are small. The dorsum in winter pelage is pale brown to grizzly black and paler in summer; there is one whitish stripe along each side of the body. The skull is wide postorbitally, the bullae are inflated, and the braincase is relatively flattened, with a gentle slope from the highest point posteriorly to the lambdoidal crest (Fig. 2). The masseteric tubercle is small and directly below the infraorbital foramen, and the outer edge of the infraorbital foramen is inclined slightly ventromedially. The interorbital foramen always is present and large (Hoffmeister, 1986). Each foot has five toes. On the forefoot, the thumb is reduced to a small tubercle with a blunt nail; the second toe is longest. On the hind foot, the middle toe is longest. On all toes, the claws are slightly compressed and a little curved. The eyes are of moderate size and placed midway between the point of the nose and the root of the ear; a white ring encircles the eye, giving it a spectacled appearance (Neal, 1964a). A. harrisii has a small and delicate head. The neck is long and the body is slender. The legs are long and a few long hairs fringe the hind parts of the forelegs (Audubon and Bachman, 1854).

The dental formula is i 1/1, c 0/0, p 2/1, m 3/3, total 22 (Ingles, 1965). The teeth are rather small and the lower incisors slightly curved. The incisors are yellowish. Whiskers and nails are black and the back and sides are minutely speckled with white, on a yellowish-brown background. The hairs are dark-brown at the roots,

then white, then black, and the tips are brownish-white, with a tinge of vellow. On the nose and forehead, the speckled appearance of the back is superseded by a rufous tint. Between the ears, on the neck, and a little downwards towards the legs, grayish-white is the prevailing color. A narrow white stripe rises from behind the shoulder and runs along the side of the back to the middle of the hips. Color around the eye, throat, chin, inner surface of the legs, and the whole underside of the body is whitish, with a few black hairs interspersed. There is a tinge of brownish-red on the outer surface of the forelegs that is more strongly red on the thighs. The feet and outer surface of the legs are yellowish-white. Hairs of the tail are whitish at the roots, twice annulated with black, and tipped with white. There is a line of whitish-yellow on the flanks, distinctly separating the color of the back and sides from the undersurface, and extending along beneath the reddish-brown tint on the thighs where it becomes a deeper yellow (Audubon and Bachman, 1854).

Hairs on the back are short and somewhat coarse, but lay smoothly, giving the animal a glossy appearance. On the undersurface, they are coarse and rigid. On the hind feet, the middle toes are longest, the two on each side being of nearly equal length, the outer considerably shorter and the inner shortest. The feet are covered with short hairs that do not conceal the nails. The soles of the feet are tuberculate (Audubon and Bachman, 1854).

The forehead is reddish-gray, the neck is ashy-white running into yellowish iron-gray on the back, and the undersurface is ashy-white. The tail is of moderate length and has long hairs growing from the side. The color is uniformly a mixed black and white. The outer surface of the face and hind legs are pinkish cinnamon. Upper parts (except stripes) are grayish with ochraceous. Black vibrissae occur on the upper eyelid (4-5), upper lips (about 12), and on the cheek (4-5). The upper and lower eyelashes are of equal length (Neal, 1964a).

There are no differences in external and cranial measurements between sexes. Range of means of nine populations and extremes for individuals (in mm) of 39 males, 36 females, and 2 of unknown sex from Arizona and Sonora are: total length, 229.0–245.8 (216–



Fig. 1. Photograph of Ammospermophilus harrisii. Courtesy of the Arizona-Sonora Desert Museum.



Fig. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of *Ammospermophilus harrisii* (male, from near Ajo, Maricopa Co., Arizona). Greatest length of cranium is 39.5 mm. Photographs by T. L. Best and J. L. Dobie.

267); length of tail, 70.9-84.6 (67–92); length of body, 147.5-162.0 (137–178); length of hind foot, 37.2-41.6 (35–46); length of ear, 11.5-13.9 (10–16); greatest length of skull, 39.2-41.0 (37.6–42.4); palatilar length, 17.4-18.2 (16.6–19.1); zygomatic breadth, 22.7-23.7 (22.0–24.1); cranial breadth, 18.8-19.7 (18.1–20.5); interorbital breadth, 9.0-9.8 (8.5–10.4); postorbital constriction, 13.1-14.3 (12.2–14.9); nasal length, 11.5-12.8 (10.2–13.6); length of maxillary toothrow, 7.0-7.3 (6.5–7.8); bulla length, 10.2-10.9 (9.8–11.4; Hoffmeister, 1986). The average mass of 55 males and 48 females from southern Arizona is 122 g for each sex (Neal, 1965a). The ratio of tail to body averages 52 to 59 (Doutt, 1934)

Geographic variation is primarily in size. Western populations display little interlocality variation, while there is a general size

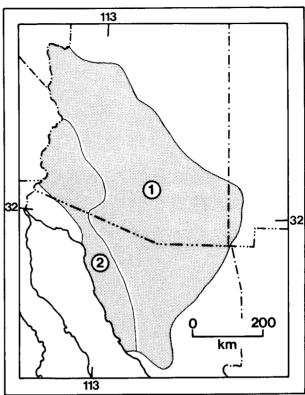


Fig. 3. Distribution of Ammospermophilus harrisii in western North America (Hall, 1981): 1, A. h. harrisii; 2, A. h. saxicolus.

increase in northeastern populations. Pelage coloration has higher eumelanin content in populations in more mesic regions (Hafner, 1981). The subspecies A. h. saxicolus, found on the lower desert plains of southwestern Arizona and northwestern Sonora, is paler in color than A. h. harrisii of the Tucson region, but the difference in color tone between the two subspecies is slight. Tint-photometer readings for reflected red of A. h. saxicolus from southwestern Arizona and northwestern Sonora average 16.0% (13–20), while A. h. harrisii from near Tucson average 14.4% (13–17); the difference is not statistically significant (Dice and Blossom, 1937).

DISTRIBUTION. Ammospermophilus harrisii occurs below 1,350 m elevation (Hoffmeister, 1956) in the southwestern United States and northwestern Mexico (Fig. 3). The Colorado River may function as a barrier or at least a dispersal filter where it divides A. harrisii and A. leucurus. This river does not appear to inhibit dispersal of A. leucurus above the central Grand Canyon of Arizona, after which point A. harrisii is no longer found on the opposite side (Hafner, 1981). An aqueduct near Phoenix, Arizona, does not impede movement of A. harrisii (Campbell, 1981).

FOSSIL RECORD. The genus Ammospermophilus probably diverged in the Miocene and had already attained nearly modern form by Clarendonian times (James, 1963). No fossils of A. harrisii are known.

FORM AND FUNCTION. The cheekpouch is large, extending posteriad to the level of the manubrium sterni (Bryant, 1945). The ears are somewhat triangular, and thinly covered with short adpressed hairs (Neal, 1964a). The ears are short and broad, and do not project dorsally to the level of the head. The pinna is rounded and its width is equal to or greater than its height. There is no antitragus or intertragal notch. The length of tail is 25–33% of the total length, and the legs are relatively long. The soles of the feet are heavily haired. The cranium is nearly quadrate. External margins of the infraorbital foramina usually are vertical with the bases directed ventrolaterad, and the masseteriic tubercules situated ventral or slightly ventrolateral to the foramina. The zygomatic plate forms an angle of about 50°. There are 19–20 caudal vertebrae (Bryant, 1945).

Cuticular scales on the hairs are more flattened than mosaic

in form (Short, 1978). Winter pelage is longer and softer than summer pelage, which is harsh and consists of closely spaced hairs. There are two molts. The spring molt occurs in May or June (Hoffmeister, 1986); on 13, 16, and 19 May, animals were in badly worn condition, with new hair occurring in patches all over the body (Howell, 1938). Animals in August are still in summer pelage. The autumn molt apparently takes place in October; on 23 September, one female was in summer pelage and those seen on 30 October were in winter pelage. Juveniles first appear above ground in summer pelage (Hoffmeister, 1986).

In winter pelage, the general tone of upper parts is mouse gray with the hairs fuscous subterminally and conspicuously tipped with white. The head and face are vinaceous buff or fawn color; shoulders and thighs are vinaceous fawn, front legs and feet are vinaceous cinnamon, hind feet are pale vinaceous-cinnamon, and the toes are pinkish buff. The tail above and below is mixed with black and white, the hairs with a broad subterminal band of black and a narrower black band near the base. In summer pelage, the upper parts are nearly uniform pale pinkish-cinnamon, clearest on shoulders and thighs, somewhat darkened with fuscous on the back (Howell, 1938).

One male and two albino females were captured near Ajo, Maricopa Co., Arizona. They had white pelage, pink eyes, and flesh-colored feet. The two females were held in captivity and were healthy and vigorous, but produced no young in 4 years although a normal male and female were in the same cage. The albinos were shyer than normal ones, possibly attributable in part to a greater sensitivity to light (Neal, 1964b).

Even when supplied with abundant food in captivity, A. harrisii stores little body fat. There is little fluctuation in body weight throughout the year (Neal, 1965a).

The adrenal glands of A. harrisii average two or three times the size of those in Spermophilus tereticaudus. Adrenal weights in male A. harrisii reach a peak about 1 month before that of females. In females, the maximal adrenal size occurs during March, April, and May (Neal, 1965a); this pattern corresponds to the early breeding season of A. harrisii (Neal, 1964a). After reaching maxima during the breeding and reproductive season, adrenal weights in both sexes decline, but the adrenal glands tend to increase during the winter months and do not involute (Neal, 1965a).

The mean rectal temperatures of young (38.4–40.0°C) are slightly lower than those of adults (39.5–40.3°C) during the same months. The annual range of rectal temperatures for adults is from 35.3 to 41.6°C; for young the annual range is from 37.6 to 41.7°C. There may be a correlation between body temperature and air temperature during the warm months of June and July (Neal, 1965a). The lethal temperature is from 35 to 45°C. Changes in body temperature from the average of 38.6°C (range, 35.3–39.8) for various temperatures were: at a temperature of 5°C, the change was -5.7° C; at 15° C, -3.0° C; at 25° C, -0.7° C; at 35° C, -0.5° C; at 40° C, -0.3° C for one animal and two others died; and at 45° C, the three experimental animals died (Neal, 1964a).

The respiratory rates of two resting A. harrisii were 160 and 166/min (Neal, 1965a). Oxygen consumption at 20°C in August averaged 2.14 cc $O_2^{-1}g^{-1}h^{-1}$ (range was from 1.67 for an immature male to 2.58 for an adult female). At 30°C in August, it averaged 2.04 cc $O_2^{-1}g^{-1}h^{-1}$ (range was from 1.77 for an adult female to 2.35 for an immature male). At 30°C in December, it averaged 1.65 cc $O_2^{-1}g^{-1}h^{-1}$ (range was from 1.45 for an adult male to 1.96 for another adult male; Neal, 1964a).

Hematocrit values ranged from 16.0 to 71.0 (average, 38.6). The hematocrit of A. harrisii does not differ from that of Sigmodon hispidus, but there is a difference between adult males and immature animals. There are highly significant differences between the mean yearly hematocrit values of S. tereticaudus and A. harrisii (Neal and Wood, 1965).

The penis is large and fleshy (Dice and Blossom, 1937). The baculum is fan-shaped, with wide lateral proximal and distal expansions and a pronounced shaft angle. It is <2 mm in length and apparently acts only as a hardened tip to facilitate initial intromission of the penis. The bizarre fan-shape, asymmetry, and variability in number of tooth-like projections of this delicate bone would seem to have no other functional attributes (Hafner, 1981). The broad base of the bone tapers, almost entirely on the right side, abruptly into the slender shaft. Distally, the shaft broadens, gradually on the right side and rather suddenly on the left, into a circular ladle or dipperlike portion with the sides (or wings) curved back toward the base. On the dorsal edge of the circular, distal expansion are 13–17 sharp,

tooth-like projections that curve outward. There is no ventral knob or keel on the distal end. The baculum of *A. leucurus* is indistinguishable from that of *A. harrisii* (Burt, 1960).

ONTOGENY AND REPRODUCTION. Harris' antelope squirrel may breed as early as December or January (Neal, $1965\dot{b}$). A vaginal plug probably is formed after copulation. Adult males taken in April extruded at death a large amount of sticky fluid from the penis, and this fluid soon hardened into a solid mass (Dice and Blossom, 1937). In southern Arizona, the earliest indication of spermatogenesis was on 4 November; a sperm smear revealed tailed spermatozoa in the seminiferous tubules. The last male possessing live spermotozoa was examined on 16 June; this individual had only a few inactive sperm cells present. Testes regress in size in June and July to <10% of the February and March mass. The first evidence of the beginning of the breeding season in females was observed in two adults on 18 February. Both had swollen labia and enlarged uteri, but imperforate vulvae. The first female with embryos was observed 23 February; she contained six embryos (uterine swellings 8 by 8 mm). One of two females examined on 25 February had swollen labia and an open vaginal orifice; the other had an open vaginal orifice, but the labia were not so swollen. A pregnant female with swollen labia and open vaginal orifice was livetrapped 2 March. She was confined in a cage and gave birth to six young 29 days later (31 March). Assuming a gestation period of 30 days, she probably mated during the last week of February (Neal, 1965b).

Ammospermophilus harrisii gives birth to only one litter per year (Neal, 1965b). However, two females from near Tucson on 16 and 17 April were lactating, and it is possible that a second brood may be reared during the same season. On 21 March, a male at the same locality had testes that were greatly enlarged. Other males in mid-April had large testes, and were in breeding condition (Dice and Blossom, 1937).

Before parturition, females in captivity prepare a round nest in cotton material. Frequently the top of the nest is completely covered with cotton, leaving only one hole open for entry and exit. At other times, the top is left so the young are exposed when the female is off the nest (Neal, 1965c). The average litter size is 6.5 (Neal, 1965b). Dates and information on embryos are: 8 January, nine embryos (Allen, 1895); 17 February, six large fetuses (Mearns, 1896); 5 March, six embryos (Grinnell, 1914); 15 March, five embryos about 15 mm in length (Dice and Blossom, 1937); 20 March, six fetuses the size of small grapes (Bailey, 1931); and 5 April, six embryos representing the latest pregnancy (Neal, 1965b).

Mass at birth averages 3.6 g (range, 3.0-4.1). Rate of growth varies from an increase in mass of 9.3%/day during the first 2-3 weeks to 0.16%/day as adult size is approached after about 7 weeks. Adult mass is achieved at the following rates: 25% is completed by 38 days; 50% by 56 days; 75% by 75 days; 90% by 150 days; and 100% by 217 days. Initially, the hind feet grow more rapidly than other body dimensions attaining 50% of adult size by 23 days and 90% in 63 days, length of head and body reaches 50% in 24 days and 90% in 87 days, and length of tail reaches 50% in 30 days and 90% in 217 days. Length of head and body can be used to estimate age up to 7 months (Neal, 1965c).

Newborn are naked and the skin is pink and rather transparent. Young cannot crawl, but they can right themselves when placed on their backs. Eyes and ears are not open. Vibrissae are evident around the muzzle. The umbilical cord is lost on the first day. Sex of the young can be determined the first day. At 1 week, the dorsal sides of the head and back are covered with black pigmentation, and young defecate small yellow fecal pellets. At 2 weeks, two pale stripes are distinguishable on the black-pigmented back; these stripes are covered with white hairs in the adult. The dorsal side of the head is beginning to be covered with short, fine hairs. With the exception of vibrissae, new hairs appear first on the dorsal side of the head. At 3 weeks, claws are well developed and lower, but not upper, incisor teeth have erupted. The young still cannot walk without falling over. The scrotum of males is quite dark in contrast to the rest of the body. Young are very vocal even at this age and frequently utter a half-muffled trill, especially when they are disturbed as in handling. Between 3 and 4 weeks, the ears open, the young are fully covered with short hairs, and at this stage resemble adults. At 4 weeks, the lower incisors are fully erupted, and the upper incisors are beginning to erupt. No premolar or molar teeth are present. The young are still vocal; the trill is similar to that of adults. When trilling, the young generally stand upright and shake all over. At

this age they still cannot run well and usually wobble a great deal when running. Eyes open from 29 to 34 days; running and other movements improve a great deal when the eyes first open. At 5 weeks, the young still nurse and pass yellow feces. At 7 weeks, the young begin to pass dark fecal pellets. They apparently are weaned by this time, since the young do not nurse after 7 weeks and the teats of the adult female shrivel and appear to be inactive. The dark-colored fecal pellets apparently indicate a change from a milk to solid diet at the time of weaning. Young first emerge from their burrows between 4 and 5 weeks of age, when the eyes have just opened (Neal, 1965c).

In the lower Colorado Valley, no young were observed from 25 February to 9 April (Grinnell, 1914). However, a family of at least three half-grown young was seen in Sonora on 27 March (Dice and Blossom, 1937). By the middle of July there are half-grown young (Bailey, 1931), and in the Graham Mountains, Arizona, one young-of-the-year had nearly attained adult size by mid-August (Hoffmeister, 1956).

Young-of-the-year are recognized by small size, pelage color, small-unpigmented nipples, and undeveloped gonads. In southern Arizona, young are first observed in May when they are about 2 months old. They increase in weight until August and then stay at about 100 g for the next 3 months. At 3 months of age, it is difficult under field conditions to distinguish young-of-the-year from adults (Neal, 1965a).

Males have scrotal testes by week 14-19. The testes become large and pendant and remain in this condition until 28 weeks of age (early October), at which time they become abdominal again. Apparently, they reach active breeding condition at this time. Thus, males may reach sexual maturity during their first year. Females do not come into breeding condition until the spring following their birth (at about 10-11 months of age). The vagina does not open until the female is in heat (Neal, 1965c).

ECOLOGY. Ammospermophilus harrisii occupies a variety of desert habitats, including areas with cacti and desert shrubs (Fig. 4). It is the most conspicuous small diurnal mammal of the desert plains from Tucson to the Colorado River, but it has a spotty distribution (Dice and Blossom, 1937). The burrows usually are under a desert shrub, such as palo verde (Cercidium), mesquite (Prosopis), or creosotebush (Larrea), but sometimes they are in the open (Doutt, 1934). In the lower Colorado Valley, Harris' antelope squirrels are in rocky areas in the rough hills and on those parts of the desert mesa where the wind keeps the weathered detritus removed, leaving a surface of firmly packed gravel or pebbles (Grinnell, 1914). Near Scottsdale in southern Arizona, A. harrisii occurs on relatively flat, sandy to gravelly desert covered with Larrea tridentata and Atriplex polycarpa (Clothier, 1960). In the Chiricahua Mountains of southeastern Arizona, it is numerous only in the black lava foothills (Cahalane, 1939). In southwestern Arizona and western Sonora, it inhabits bare, granite mountain ranges (Mearns, 1896). South of Tucson, it occurs on sandy soil dominated by mesquite, palo verde, grass, and cholla cactus (Opuntia). North of Tucson, it occurs on rocky ledges and rocky hillsides (Dice and Blossom, 1937). A. harrisii is numerous in the Tucson Mountains where the dominant plants are Carnegiea gigantea, Cercidium microphyllum, Franseria deltoidea, Simmondsia chinensis, Fouquieria splendens, Opuntia engelmanni, Echinocactus wislizenii, Prosopis juliflora, and Acacia greggii (Neal, 1964a). In Sonora, it is found in the Larrea-Franseria, Opuntia-Cercidium, Bursera-Jatropha, Olneya-Encelia, and Acacia-Prosopis vegetative associations. Habitat includes open areas in plains, valleys, canyons, and river bottoms (Caire, 1978).

Harris' antelope squirrel has an average range of movement of 274 m/individual. In a southeastern Arizona study area, density ranged from 0.08 to 0.36/ha, with greatest densities from late spring to late summer (0.24-0.36/ha) and least densities from autumn to early spring (0.08-0.24/ha; Chew and Chew, 1970).

Ammospermophilus harrisii is omnivorous (Morton, 1979). In New Mexico, its food is mainly the fruit and seeds of cactus, but numerous other seeds and green plants are eaten. In Arizona, it feeds on mesquite beans and seeds of yuccas (Yucca; Bailey, 1931). In the Graham Mountains, it feeds on fruits of the prickly pear cactus (Opuntia). Its forepaws, faces, intestinal tracts, and muscles may be stained from the juices. These squirrels may suffer from the pricks of the small, sharp spines on the fruits of this cactus (Hoffmeister, 1956). It feeds on seeds of the screw-pod mesquite and one

had its cheekpouches distended with the shelled beans (Allen, 1895). Capacity of the cheekpouches is considerable; one contained 44 beans of *Prosopis* (Mearns, 1907). One individual was observed feeding at a pile of horse dung that contained many undigested mesquite seeds (Doutt, 1934). Trapped specimens of small mammals may be consumed by *A. harrisii* (Swarth, 1929).

Ammospermophilus harrisii is widely sympatric with Spermophilus tereticaudus. Both species are found in large numbers west of Oracle, Pinal Co., Arizona. Dominant plants there include Opuntia spinosior, O. fulgida, O. engelmanni, Echinocactus wislizenii, Prosopis juliflora, and several species of grasses. Both species of ground squirrels are found only a few meters apart, and in several instances were observed entering the same Dipodomys den. A. harrisii selects areas where vegetation is dense, but S. tereticaudus favors more open habitat along roads and near Dipodomys dens. At other areas in southern Arizona, A. harrisii inhabits rocky hillsides or rocky soils and S. tereticaudus occurs only 50 m away on flat Larrea habitat where soils are sandy (Neal, 1964a).

Associated mammals include Sylvilagus auduboni, Lepus californicus, Thomomys umbrinus, Dipodomys merriami, D. spectabilis, Peromyscus maniculatus, P. eremicus, Urocyon cinereo-argenteus, Lynx rufus (Clothier, 1960), Spermophilus spilosoma, Thomomys bottae, Sigmodon hispidus, Dipodomys ordii, Chaetodipus penicillatus, C. hispidus, Perognathus flavus, Reithrodontomys megalotis, R. flavescens, Onychomys leucogaster, O. torridus, Neotoma albigula (Brown and Zeng, 1989), Notiosorex crawfordi, Lepus alleni, Perognathus amplus, Chaetodipus baileyi, C. intermedius, C. goldmani, Dipodomys deserti, Peromyscus crinitus, P. merriami, Neotoma lepida, Vulpes macrotis (Hafner, 1981), Canis latrans, Taxidea taxus, Odocoileus hemionus, and Ovis canadensis (Goldman and Moore, 1946). Reptiles occupying the same geographic area include Gopherus agassizi, Coleonyx variegatus, Xantusia vigilis, Sauromalus obesus, Dipsosaurus dorsalis, Callisaurus draconoides, Gambelia wislizenii, Sceloporus magister, Urosaurus graciosus, Uta stansburiana, Phrynosoma, Cnemidophorus tigris, Heloderma suspectum, Masticophis flagellum, Arizona elegans, Lampropeltus getulus, Crotalus molossus, and C. scutulatus (Hafner, 1981).

The fungus Coccidioides immitis was found in cultures taken from A. harrisii in Arizona (Emmons, 1942). Parasitic nematodes frequently occur in the stomach, small intestine, caecum, and infrequently in the large intestine (mixed with fecal pellets) and mesenteries of the visceral cavity. Nematodes from the caecum of an adult male from the Santa Rita Mountains were Citellina triradiata (Neal, 1964a). Ectoparasites include: the fleas Thrassis arizonensis (Augustson, 1955; Tohm, 1953), T. gladiolis (Hubbard, 1947), T. setosis (Hubbard, 1947; Tohm, 1953), and Echidnophaga gallinacea; the lice (Anoplura) Enderleinellus suturalis and Neohaematopinus citellinus (Beer et al., 1959); and the tick larvae Ornithodoros talaje (Neal, 1964a). Statistics of occurrence for E. suturalis on two males and five females of A. harrisii, respectively, were: percent infested, 50 and 60; total lice, 83 and 292; and average lice per infestation, 83 and 97 (Beer et al., 1959).

BEHAVIOR. Ammospermophilus harrisii has been the subject of zoo exhibits (Dolan and Moran, 1969) and is a diurnal animal that is active throughout the day (Swarth, 1929), including the hottest part of the day (Doutt, 1934). A. harrisii terminates its activity approximately 20 min (range, 14–45) before D. merriami begins its surface activity (Schwab, 1966). It does not hibernate (Neal and Wood, 1965), and is active above ground in each month of the year (Neal, 1965a).

Harris' antelope squirrels are never found abundantly, but singly, as individuals here and there. Their centers of habitation are near rock-bound hills, where safe shelters are to be had. At times they are seen atop bristling-spined cholla cactus (*Opuntia*), where they sit erect to view the surrounding area. How they negotiate the climb over the thorns is a question, for the soft pads of the feet never contain spines nor are there scars to indicate former difficulties (Huey, 1942).

Ammospermophilus harrisii is a vigorous runner, with sharply delineated activity and rest periods, under most lighting conditions. The species is strongly diurnal in all L/D schedules in the laboratory (DeCoursey, 1973). It runs about the desert floor, stopping frequently to dig up something from the ground. The shallow holes it leaves are evident signs of its presence (Doutt, 1934). A. harrisii shells



Fig. 4. Habitat of Ammospermophilus harrisii west of Tucson, Pima Co., Arizona. Photograph by T. L. Best.

beans of *Prosopis* before taking them into the burrow. This stored food accounts for the somewhat rare appearance of the squirrels above ground during the coldest weather (Mearns, 1907).

This antelope squirrel commonly sits up perfectly erect upon its hind feet. When disturbed, it runs carrying its tail straight up in the air, uttering chipperings as it hurries to nearby shrubbery to enter a burrow; before escaping it often stops, calls, and stamps with its forepaws (Mearns, 1907). As in other Ammospermophilus, the alarm call is a trill; ontogeny, sex, temperature, or season do not affect call characters. Duration of call, band of frequencies emitted at onset, frequency of the fundamental, and lowest frequency are highly correlated with measures of the rostrum. Long pure-toned alarm calls of A. harrisii may have originated in the last 10,000 years in response to the increasingly sparse desert vegetation (Bolles, 1981). The calls are high-pitched, long, with a wide pulse rate, and no "kuk." The long pure-toned trill of A. harrisii appears to be adapted to open desert conditions. Means of characters of alarm calls are: length of call from first sound emitted to end of call, 2.24 s (range, 1.30-3.88); frequency band around trill at onset of call, 2.22 kHz (0.60-6.50); mean pulse duration, 0.050 s (0.030-0.057); frequency of main sound energy of the trill one-half way in its duration, 2.73 kHz (1.80-3.20); cascade ratio, 1.01 kHz (0.86-1.47); lowest frequency emitted, 1.46 kHz (0.00-2.60); frequency of the fundamental, 2.03 kHz (1.10-3.30); frequency of trill at beginning, 2.69 (1.80-3.30); frequency of first harmonic above main sound energy, 4.62 kHz (3.40-5.70); and length of trill from first clearly configured pulse to end of call, 2.25 s (1.30-3.88; Bolles, 1988). A. leucurus and A. harrisii have the largest number of derived characters of alarm calls of the five species of Ammospermophilus (Bolles, 1980).

Three half-grown young were observed near water holes in Sonora. Numerous tunnels ran under the rocks where the squirrels were playing and abundant deposits of feces lay at the entrances to some of the tunnels (Dice and Blossom, 1937).

There is an extreme effect of operant level on conditioned



Fig. 5. Karyotype of Ammospermophilus harrisii (Hsu and Benirschke, 1971).

licking. Regardless of level of water deprivation, the apparatus is an apparent soporific for the squirrels. Licking is sporadic and conditioning is negligible (Boice, 1968).

GENETICS. As in other members of the genus, the karyotype of A. harrisii has a diploid number of 32 chromosomes (Fig. 5; Nadler and Sutton, 1962). There are three pairs of chromosomes bearing interstitial blocks of heterochromatin, and one small and two large pairs of subtelocentrics in which the major portions of the long arms are heterochromatic. In some cells, one of these pairs appears to have heterochromatin extending from the centromeres to about one-third of the way down the long arms. There are two pairs of submetacentric chromosomes with heterochromatin extending from their centromeres to one-half way down their long arms. The Y chromosome of A. harrisii also is heterochromatic (Mascarello and Mazrimas, 1977). In pachytene cells, some bivalents have large asynaptic regions. The number of asynaptic regions never exceeds one per bivalent nor three per cell; these regions occur in 61% of the pachytenes (Mascarello, 1980).

There is 11.4 pg of DNA per cell nucleus in *A. harrisii*. Cesium-chloride buoyant-density gradients suggest the DNA exhibits two prominent satellite peaks with densities of approximately 1.708 and 1.717 g/ml (Mascarello and Mazrimas, 1977). The satellite DNAs are characterized as: alpha, 1.708 g/ml; beta, 1.717 g/ml; and gamma, 1.707 g/ml (Mazrimas and Hatch, 1977).

Electrophoretic data indicate relatively low levels of genetic divergence among species of *Ammospermophilus*, with a mean Nei genetic distance measure of D = 0.05. *A. harrisii*, *A. leucurus*, and *A. insularis* are least different (D = 0.004–0.026; Bolles, 1981).

REMARKS. Based upon phenetic clustering of cranial and postcranial skeletal morphology, A. harrisii is more similar to A. interpres than it is to A. leucurus or A. nelsoni (Hafner, 1984). The C-banding pattern of chromosomes of A. harrisii resembles those of A. insularis, and the G-banded karyotypes of these species are more similar than between any other pair of species of Ammospermophilus. Chromosome banding similarities indicate that A. harrisii may be closely related to A. insularis (Mascarello and Bolles, 1980). The G-band comparisons of Mascarello and Mazrimas (1977) imply that the karyotype of A. harrisii may be the most primitive of the genus.

Ammospermophilus is derived from ammos referring to sand, spermatos alluding to seed, and philos meaning loving or desiring affinity (Jaeger, 1955). The specific epithet harrisii honors Edward Harris (Audubon and Bachman, 1854). The common names used by Audubon and Bachman (1854) were "Harris's Spermophile" and "Marmot Squirrel"; others include grey-tailed antelope squirrel (Bailey, 1931) and Yuma antelope ground squirrel (Hoffmeister, 1956).

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